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Observations of deep-sea octopodid behavior from undersea vehicles*

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Abstract: Despite high octopodid diversity in the deep sea, the few opportunities to observe these animals *in situ* limit tests of behavioral predictions made from anatomy. Over the last decade, I have made numerous opportunistic observations of these octopuses using submersibles and remotely operated vehicles. Most commonly seen were octopuses near hydrothermal vents in the North Pacific Ocean at greater than 2200 m depth. Despite the potential submersible-created artifact, the observed behaviors of octopuses of the genera *Benthoctopus* Grimpe, 1921, *Graneledone* Joubin, 1918, and *Vulcanoctopus* González *et al.*, 1998 are reported here. *Benthoctopus* and *Graneledone* differ in wariness and in egg-brooding postures, although both genera produce large eggs from which male hatchlings emerge with clearly developed copulatory arms. In a behavior interpreted as foraging for infauna, octopuses of both genera move the mid-section of their arms through the upper sediment. *Graneledone* seems more common, perhaps because individuals are typically larger and move more slowly. The greater wariness of *Benthoctopus* increases the species' propensity to jet and limits observations and capture. Despite considerable submersible time spent in their habitat, octopuses of *Vulcanoctopus* remain little known; only male specimens are available for study. The few data available indicate that deep-sea octopuses take small prey, as Voss (1988) predicted based on the lack of the esophageal crop and the small posterior salivary glands. If deep-sea octopuses rely on small prey, the need for a crop to serve as a food storage organ is minimized, as is the need for glands that produce venom to subdue large and potentially dangerous prey.

Key words: *Benthoctopus*, *Graneledone*, *Vulcanoctopus*, North Pacific Ocean, embryos

Deep-sea octopodids, defined here as occurring at greater than 2000 m depth, are surprisingly diverse (Voss 1988). Our knowledge of the biology of these animals, however, is limited by the rigors imposed by the deep-sea habitat. The darkness, cold, and high hydrostatic pressure define the habitat and prohibit its direct exploration by air-breathers. In addition to these deep-sea features, the unpredictable distribution of the animals and the expense of conducting research in the deep sea mean that most observations of the animals in nature must be opportunistic. Most type specimens were pulled dead from trawl nets and preserved at sea without being seen by specialists. This contribution summarizes our current, minimal knowledge of deep-sea octopodids and offers a starting point for future research.

Comparative anatomical studies of the Octopodidae reveal apparent convergences among deep-sea benthic octopuses (Voss 1988). The ink sac, a symplesiomorphy of the cephalopods that is thought to be associated with defense against visual predators, is lost. Morphometric studies find that deep-sea and high-latitude octopuses tend to have short arms and small suckers compared to octopuses from shallow water and low latitudes (Voight 1993). Features of the anterior digestive system, including the esophageal crop, radula, and posterior salivary glands, are small or absent in deep-sea octopuses, a pattern that Voss (1988) attributed to their diet of small prey. Although its function was not explicitly stated by Voss, the crop may primarily serve to store food rather than digest it, and large posterior salivary glands produce the venom that immobilizes large, dangerous prey that deep-sea octopuses rarely encounter.

This report summarizes my observations of deep-sea octopuses made over the last decade during research cruises, and images made available by participants in other cruises. The deep-sea octopodid genera *Benthoctopus* Grimpe, 1921, *Graneledone* Joubin, 1918, and *Vulcanoctopus* González *et al.*, 1998 are the subjects of the observations.

MATERIALS AND METHODS

Observations of seafloor animals such as octopuses *in situ* require use of the crewed Deep Submergence Vehicle *Alvin* or Remotely Operated Vehicles (ROVs) such as *ROPOS*, *Jason*, or *Tiburon*. Towed cameras that are lowered from a surface ship to a few tens of meters above the bottom to take images at pre-set intervals also can document benthic octopuses. Regardless of the technique used, undersea assets require bright lights and cameras to detect and record the presence and/or behaviors of any deep-sea animals encountered. The behaviors observed therefore are presumed to be

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typical, as no observations can be made without the lights and other disturbances the subsea vehicle creates.

Most dives, and thus most observations, reported here took place in the North Pacific Ocean, in or near hydrothermally active areas of Juan de Fuca and Gorda Ridges, generally at depths of 2000 to 2650 m. A few observations were made near 1550 m depth inside the caldera of Axial Volcano on Juan de Fuca Ridge. Because hydrothermally active areas are of interest to geophysicists, geochemists, biologists, and others, a disproportionate amount of the available submersible and ROV time is spent there. Observations also derive from submersible and ROV dives that targeted off-axis rocky outcrops, such as Baby Bare and Wuzza Bare near 2600 m depth on the Cascadia Basin and Mendocino Ridge at depths of 1550 m. Observations of *Vulcanoctopus* were made on the East Pacific Rise, between 8.5° and 11°N near 2550 m depth.

Observations made during the 17 submersible and ROV cruises in which I participated contribute to this report and are supplemented by photographic and video images provided by other researchers and by submersible crews. Several researchers, notably V. Tunnicliffe and R. Embley, kindly allowed me access to their compiled seafloor images. In addition, some researchers provided octopus image(s), without any comment on the frequency with which the animals were encountered or the total duration of bottom time. Although providing vital information, these sources limit attempts to estimate the frequency with which octopuses were detected, or with which a given behavior was observed. In addition, the density of octopus on the deep-sea floor is not uniform (Voight 2002). In some areas, aggregations of brooding octopuses reached extremely high densities (Voight and Grehan 2000, Drazen *et al.* 2003), yet in "normal" seafloor areas, hours of bottom time may be required before a single octopus is seen.

The observations reported here are by their nature *ad hoc*, as are the collections. Other than brooding octopuses, the longest observations were made of individuals that could not be collected. Conversely, often only minimal observations could be made of collected individuals, as they were collected nearly as soon as they were detected. Octopuses were collected in two ways. Large octopuses were grabbed by the submersible's manipulator arm and placed inside lidded boxes. Smaller octopuses were more often collected in a suction sampler. Octopuses were preserved in buffered formalin in seawater and are catalogued in the collections of The Field Museum, Chicago, Illinois. Catalogue numbers can be accessed through the online database at http://emuweb.fieldmuseum.org/iz/mollusks.php. Mantles of preserved octopuses were opened; if the stomach or esophagus appeared full, the organs were also opened and their contents examined under a dissecting scope.

Characters diagnostic of genera (Voss 1988, González *et al.* 1998) that could be detected without examining the specimen in hand were used to identify the octopuses to genus, with the assumption that the ink sac was absent. Octopuses in the Northeast Pacific with a single row of suckers or with suckers arrayed in a zigzag line, prominent supraocular cirri, and textured dorsal mantle were assigned to *Graneledone* Joubin, 1918 (Fig. 1), the only octopodid genus with a single row of arm suckers known from the North Pacific (Voss 1988). The identity of some specimens with zigzag sucker rows was ambiguous after only brief observation, although with extended observations, the texture of the dorsal mantle and the presence of supraocular cirri were nearly always sufficient to resolve any ambiguity. A mantle fold was seen on some individuals, although this character is not considered to be typical of this genus. Two species of this genus have been described from the east and west North Pacific (Nesis 1982, Voss and Pearcy 1990). Although these species were synonymized by Hochberg (1998) as *Graneledone boreopacifica* Nesis, 1982, because cryptic species may exist, I assigned all individuals to the genus rather than a given species.

Pigmented octopuses with double sucker rows were assigned to *Benthoctopus* Grimpe, 1921 (Figs. 2-3), as the only members of this deep-sea genus have been described from greater than 1000 m depth north of 40°N in the Pacific. The dorsal surface of all members of this genus is thought to be smooth, and none of the available observations indicated otherwise. Among octopuses attributed to *Benthoctopus*, four apparent species could be distinguished. The largest species had long arms and strong reverse counter-shading (Fig. 2); two seemingly moderate-sized, uniformly colored species were distinguished by differences in eye size. The fourth species was *Benthoctopus canthylus* Voss and Pearcy, 1990 which was identifiable by the dramatically enlarged suckers on the dorsal arms (see photos Norman 2000: 210).

White octopuses with a double sucker row (Fig. 4) observed near hydrothermal vents on the East Pacific Rise (EPR) from 8.5°N to 13°N were assigned to *Vulcanoctopus hydrothermalis* González *et al.*, 1998. Their double sucker rows, the unusually translucent white mantle, long thin arms with an uneven surface, and small dark eyes that contrasted strongly with skin color supported the identification. Because the EPR is the type locality for the only known species in the genus, referring these octopuses to that species is conservative.

RESULTS AND DISCUSSION

Seafloor observations of benthic octopuses tend to be unusual, even rare, except in areas where brooding octopuses aggregate (Voight and Grehan 2000, Drazen *et al.*

2003). The large size and similarity of deep-sea octopuses to those of shallow-water, however, mean that deep-sea scientists, regardless of specialty, are often able to recognize the animals. The comparative rarity of octopuses makes observations memorable, facilitating information sharing.

Frequent reports of octopuses near hydrothermal vents, especially those with clams, have been attributed to the availability of clams as prey (*e.g.*, Mottl *et al.* 1998) or of hard substrate as a limited deep-sea resource (Voight 2000a). The occurrence of octopuses near abundant clams that host endosymbiotic sulfide-oxidizing bacteria might suggest that octopuses tolerate exposure to hydrogen sulfide, among the most common and toxic chemicals at chemosynthetic habitats. Clams that host sulfide-oxidizing endosymbiotic bacteria, however, can live in areas with very little sulfide in the water (Fisher 1995). Their extensible foot and blood with a high sulfide affinity allow clams to access sulfide deep in crevices or in subsurface water (Fisher 1995); potential clam predators might be exposed to very low sulfide levels.

Graneledone

Size and density: Most frequently observed in the North Pacific were octopuses of *Graneledone* (Fig. 1) due to their large size and comparatively slow movements. These octopuses, especially at depths greater than 2000 m, were reluctant to jet away from the vehicle. Among 49 preserved specimens, those from comparatively shallow depths (1300 to 2000 m) were typically larger (up to 59 cm total length) with longer arms carrying more suckers (up to 116 per arm) than were those from greater (to 2800 m) depths (up to 48.6 cm total length with up to 86 suckers per arm) (Voight, unpubl. data). Members of this genus were seen on sedimented ocean floor, adjacent to hard substrate, brooding eggs in aggregations on vertical rock surfaces (Voight and Grehan 2000, Drazen *et al.* 2003) but rarely near areas directly impacted by hydrothermal fluid flow. Voight (2000a) reported the global distribution of this genus in reference to areas of chemosynthetic activity.

Figure 1. Octopus of *Graneledone* photographed by fixed still camera mounted on front of the submersible *Alvin* during dive 4046 near Wuzza Bare seamount, Cascadia Basin at 2650 m depth.

Behavior: When members of this genus were seen moving across featureless sediment-covered plains, they often used the middle part of each arm as a sediment probe, in a behavior inferred to constitute foraging for infaunal prey. In this behavior, the proximal halves of the dorsal and dorsolateral arms were held nearly straight down to contact the sediment surface. The arm tips extended radially away from the octopus, remaining on top of the sediment, with the middle section under the sediment. As the octopus moved forward, it continually shifted the middle section of its arms through the superficial sediment. Several individuals performed this behavior and some preserved specimens even had a covering of sediment on the distal one-half to two-thirds of their arms. No direct observations of foraging success were possible, as the octopus would have passed any small infaunal organism it collected to the mouth by the suckers on the oral arm surface. Although such movements are very hard to confirm, slight movements of the arms toward the mouth supported the hypothesis that this behavior constituted foraging.

The guts of octopuses of this genus typically contained little. One specimen, from the caldera of Axial Volcano, had eaten snails of *Provanna variabilis* Warén and Bouchet, 1986 and polychaetes characteristic of the hydrothermal vent fauna (Voight 2000b), providing evidence that these octopus feed on small prey, in this case taken from hard substrate impacted by hydrothermal activity. An octopus collected in a non-hydrothermally active area had preyed on a small galatheid crab and a second had an amphipod in its gut.

Octopuses of *Graneledone* were often seen adjacent to hard substrate, where this substrate type was present. With most submersible dives devoted to hydrothermal vents associated with rocks, observations were biased toward hard substrate habitats. Regardless, octopuses appeared to preferentially associate with rare hard substrate in non-vent areas, such as near Ocean Drilling Program (ODP) platforms, long-term instrument deployments, and rocks. The sex and reproductive maturity of the individuals near hard substrates could not be identified.

Color: In situ seafloor observations have limited ability to identify true color, as the proximity, type, and angle of the light source can all affect the perceived color. Octopuses of *Graneledone in situ* appeared to be maroon, orange, purple, or red. Preserved specimens are purple, blue-red, or maroon in color. The skin texture of the dorsal mantle is also quite

variable among individuals, from very rugose (Fig. 1) to essentially smooth. The supraocular cirri were always the most readily seen features in terms of skin texture.

Color change was observed in two octopuses of *Graneledone*. In the better-documented observation, the octopus was between the ROV and a second octopus of *Graneledone* when half of its body blanched along the mid-sagittal line. On the other occasion, a lone octopus was approached by the ROV. It blanched, as did the individual reported above, with one side of the body colored normally and the other whitish. The contact between the colors followed the mid-sagittal line.

Egg brooding: Females of *Graneledone* that were seen brooding eggs had attached them to rocks and most often aggregated in areas with rock outcrops. Aggregations are known at 2600 m deep at Baby Bare seamount in Cascadia Basin (Voight and Grehan 2000) and at 1550 m depth on Mendocino Ridge (Drazen *et al.* 2003, Voight and Drazen 2004). Voight (2002) reports that densities of brooding octopuses at Baby Bare exceeded triple those of background areas. Males were present, though rare, among the aggregations. Brooding females invariably were positioned with their dorsal mantle facing outward and the oral surface of their arms touching the rock surface to which their eggs were attached. The total number of eggs produced is unknown, although evidence of at least 50 young was seen in one case at Mendocino Ridge (Voight and Drazen 2004), including eggs and cement from eggs that had apparently already hatched. The female that had been brooding these late-stage eggs showed signs of senescence: slack skin, cloudy eyes, and dull color. Dissection of the collected female revealed conspicuous edema of the tissues, renal organs, and an empty digestive system.

Eggs and embryos: Voight and Drazen (2004) described newly hatched embryos from an egg clutch from Mendocino Ridge that were collected as they hatched. Hatching was likely mediated by the disturbance created by collecting activities, as external yolk sacs were present within the arm crowns. These premature hatchlings were 55 mm long and males could be identified by the hectocotylus and ligula (Voight and Drazen 2004). The single intact egg collected was 39.6 mm long. Earlier, partially developed, 25 mm long ovoid eggs had been collected from an apparently conspecific female at Baby Bare at 2660 m depth (Voight and Grehan 2000). Attempts to model development time of very large cephalopod eggs are not considered to be reliable (Laptikhovsky 1999), but the large size of these eggs and the low temperatures at depth likely mean that their development occurs over a very long period (J. Drazen and B. Robison, pers. comm.). There is no indication that the females feed while brooding.

Benthoctopus

Size and density: Octopuses of *Benthoctopus* were much less commonly seen than were those of *Graneledone*. Whether the few observations of octopuses of this genus compared to those of *Graneledone* are a real difference between the densities of the genera or is, more likely, due to their smaller size, more rapid movements, and/or greater wariness cannot be assessed. The total lengths of specimens of *Benthoctopus* collected during submersible and ROV work were all under 20 cm. Members of the genus *Benthoctopus* were most often seen as single individuals on hydrothermally inactive rocks on the mid-ocean ridge spreading center (Fig. 2). Brooding aggregations were seen at two locations (below).

Behavior: Octopuses of *Benthoctopus* were observed foraging in the sediment as described above for octopuses of *Graneledone*. Individuals of *Benthoctopus*, including *B. canthylus*, were also observed to extend and hold their dorsal arms into the water column on multiple occasions. Octopuses in open, sedimented areas, and on rocks at mid-ocean ridges displayed this posture (Fig. 2). This pose was not seen to result in the acquisition of prey, but small prey may have been manipulated by suckers unobserved. The behavior could also increase chemoreception by the suckers. No octopuses of this genus were observed to change skin color or texture.

Egg brooding: Brooding females of *Benthoctopus* were found at Mendocino Ridge (Drazen *et al.* 2003) and in an

Figure 2. Octopus of *Benthoctopus* photographed by fixed still camera mounted on front of *Alvin* during Dive 4044 near GR-14 or Sea Cliff hydrothermal vent field on Gorda Ridge (North Pacific Ocean) at 2737 m depth.

extremely localized aggregation (Fig. 3) near the GR-14, or Sea Cliff hydrothermal vent field on Gorda Ridge, described by Rona *et al.* (1990). Although located near an area of hydrothermal activity, the octopuses could not be fully demonstrated to be in direct contact with the diffuse hydrothermal fluid in the immediate area. The aggregation was located in 2002 and in 2005 by the ROV *Tiburon* but could not be relocated during an *Alvin* dive in 2004. The aggregations of brooding females of both *Benthoctopus* and *Graneledone* support the hypothesis (Voight 2000a) that substrate availability limits the distribution of brooding females.

A difference between octopuses of *Benthoctopus* and *Graneledone*, based on the estimated 15 females with egg clutches of *Benthoctopus* observed, is that when brooding, these females positioned the oral surface of their arms facing outward and the arm tips in contact with the rock which held their eggs, and potentially with the eggs themselves. Females of *Benthoctopus* often brooded deeper under overhanging rocks than did the larger females of *Graneledone*, possibly due to preference or because their smaller body sizes allowed them to exploit the available niches. However, near GR-14, octopuses of *Benthoctopus* were found closely associated with a nearly vertical wall with their oral, suckered arm surfaces bent backwards to nearly cover the rest of their bodies; in one instance, an egg was visible (Fig. 3). Observations at this site were unfortunately very limited. No collections of late-stage females of this genus have been made.

Embryos: A single embryo of *Benthoctopus* was collected from near GR-14 by the ROV *Tiburon* in 2005. The large (mantle length 7.5 mm; mantle width 7; head width 5.1) embryo (FMNH 309724) had 13.1 mm long arms, each carrying about 66 suckers crowded into two rows. The hectocotylus carried 47 suckers and the ligula was clearly visible on the third right arm tip. The eyes were well developed and chromatophore organs lay just distal to the mantle openings on the lateral body, on the dorsal arm tips, and on the arm base. Few chromatophores, however, were seen on the superficial skin, as those noted on the mantle appear to have been deeper tegumental chromatophores. How near the embryo was to hatching is unclear. The preserved embryo was received with a ruptured egg capsule; the damage was likely inflicted during collection. Although there was no external yolk sac, the torn outer membrane of a yolk sac was present.

Vulcanoctopus

Size and density: Vulcanoctopus hydrothermalis was fairly common at hydrothermal vents on the EPR and at nearby non-hydrothermally-active areas. Typically, and most conspicuously, a solitary octopus was seen moving across bare basalt up to 500 m away from active hydrothermal vents (Fig. 4). Octopuses were also seen in active vent fields, often moving over the surface of giant tube worm (*Riftia pachyptila* Jones, 1981) mounds. More rarely, octopuses of *V. hydrothermalis* were seen at hydrothermal vents in aggregations (Rocha *et al.* 2002, Voight 2005). González *et al.* (2002) reported measurements of 16 individuals of this species; Field Museum specimens are within this size range.

Behavior: Most observations of octopuses of *Vulcanoctopus hydrothermalis* were brief, comprising a solitary individual moving across the basalt substrate in typical octopodid style (Fig. 4). This included random lateral movements of the arms along the surface of the substrate that may

Figure 3. Two octopuses of *Benthoctopus*, one with egg visible, photographed by ROV *Tiburon* during dive T-456 near GR-14 or Sea Cliff hydrothermal field on Gorda Ridge (North Pacific Ocean) at a depth of 2770 m.

Figure 4. Octopus of *Vulcanoctopus hydrothermalis* photographed on the East Pacific Rise by fixed still camera mounted on front of *Alvin* during Dive 3927, near 9°N at 2495 m depth.

expand the area the octopus searches for potential prey. This species is known only from 27 preserved specimens (the sum of those reported by González *et al.* 2002, and nine Field Museum specimens), all of which are male. This severely biased sex ratio suggests either that the sexes partition habitat or that females are extremely rare. Rocha *et al.* (2002) reported that five apparently male octopuses swarmed a sixth octopus, presumed to be a female, in an attempt to copulate.

Voight (2005) described feeding by a group of these octopuses in which the interbrachial web was used as a cast net to secure members of a dense swarm of the amphipod *Halice hesmonectes* Martin, France, and Van Dover, 1993. In that account, at least 12 octopuses were positioned on four extinct chimneys that nearly ringed a clump of tubeworms. The amphipod swarm, which formed in warm water over the tubeworms, was accessible to the octopuses due to the height advantage the chimneys provided. Such swarms would appear to be an unlikely standard prey for these octopuses, because swarms typically are high enough over the substrate that octopuses would be unlikely to reach them without considerable effort.

Egg brooding and embryos: Females of *Vulcanoctopus* are unknown, as are the egg-brooding habits of the species and its embryos.

CONCLUSIONS

Observations of octopuses of *Graneledone* and *Benthoctopus* apparently foraging for small infaunal animals and of octopuses of *Vulcanoctopus hydrothermalis* foraging on swimming amphipods (Voight 2005) further document that these deep-sea octopuses take small prey. They therefore support Voss' (1988) interpretation of the apparent evolutionary reductions in the anterior digestive system of deep-sea octopuses. Voss (1988) did not explicitly state the crop's function but identified the posterior salivary glands as the source of pharmacologically active venoms used by shallow-water octopus and attributed the reduction of the gland's size to the switch to small prey in the deep sea. Predators ingesting relatively small prey do not require complex venoms, as small prey can be readily subdued. Predators that take prey encountered at low densities have minimal need for food storage, as may be supplied by the esophageal crop. In addition, the radulae of octopuses that feed on bite-sized prey may serve primarily to push individual prey items into the esophagus, rather than tear off bits of venom-soaked flesh, consistent with Voss' (1988) statement that the radula is simplified in deep-sea octopuses. The comparatively small suckers of deep-sea octopuses (Voight 1993) would also function well with small prey (Smith 1996).

Although deep-sea octopuses outwardly are very similar to those of shallow water, behaviorally they have several distinctions. First, although several individuals of *Graneledone* were seen adjacent to hard structures, deep-sea octopuses were never seen to seek or use shelter, other than for egg brooding. Second, when encountered on an open sedimented plain, neither octopuses of *Graneledone* nor *Benthoctopus* made any attempt to camouflage themselves by changing either their color or skin texture. The blanching seen in two octopuses of *Graneledone* may have been a startle reaction, evidence of the presence of the chromatophore system that may be functional in some of these deep-sea octopuses not due to its current adaptive value, but to phylogenetic constraint. Freed of visual predators, deep-sea octopuses apparently rely on immobility or jetting away to evade potential predators.

All octopuses observed and collected have eyes, although those of *Vulcanoctopus hydrothermalis* are reduced (González *et al.* 1998). Because eyes are energetically expensive organs routinely lost by animals living in perpetual darkness, such as caves, their retention by deep-sea octopuses suggests that they are adaptive. One scenario in which eyes would be advantageous is if the octopuses sought bioluminescent prey. If, for example, agitating the sediment during foraging stimulates bioluminescence by infaunal animals, octopuses with eyes could be more likely to capture those prey than would those without eyes. The dark coloration of octopuses of *Graneledone* and the strong reverse ventral counter-shading seen in at least one species of *Benthoctopus* observed here may also be associated with taking bioluminescent prey as the dark ventral color would mask any light emitted from within the web. Although the presence of a light dorsal surface in some species of *Benthoctopus* has been suggested to provide crypsis against a light colored, sedimented background (Voss and Pearcy 1990), ambient light at depths of over 2000 m is negligible.

Most observations reported here were made near hydrothermal vents but cold-seep habitats also support concentrations of biomass that are sustained by chemosynthesis. Octopuses occur in these habitats (Olu *et al.* 1996, Sibuet and Olu 1998, Van Dover *et al.* 2003). Octopuses have also been recently photographed on the West Florida Escarpment seeps at near 3000 m (J. Zekely, pers. comm.), at seeps near 2330 m depth in the Gulf of Mexico (C. R. Fisher and R. S. Carney, pers. comm.). Furthermore, two different species of *Benthoctopus* have been photographed at seeps on Blake Ridge near 2000 m depth (W. Gilhooly, pers. comm.).

Major questions about deep-sea octopuses clearly remain, including life span and reproductive output. Deep-sea octopuses appear to share the life-history strategy common to most cephalopods. Octopus eggs were never found without a brooding female (and were often difficult to see due to

her ministrations). All females of both *Graneledone* and *Benthoctopus* observed with late-stage eggs were gaunt, with dull color, slack skin, and cloudy eyes; females are therefore concluded to senesce as their eggs mature. The duration of brooding remains to be determined through long-term observations. The longevity and growth rates of deep-sea octopuses are also unknown. As the logistics of undertaking such research remain difficult in shallow waters, doing so in the deep sea may remain unfeasible. With a robust phylogeny in place, comparative study of the brains of deep-sea octopuses and their color change ability might discover how the elimination of selection for crypsis has affected the nervous system and energy allocation within these deep-sea animals. Until we know the evolutionary history of the octopodids, however, discussions of adaptations or modification to the deep sea remain conjecture.

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